

Impacts of reindeer grazing and local topography on plant and lichen communities across the reindeer fence along the Finnish-Norwegian border

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Tiivistelmä - Referat - Abstract The heath vegetation in the Jauristunturit study area is highly affected by the reindeer fence that was built in the mid-1950s between Finland and Norway, to prevent summer grazing in the Norwegian side. In the study area, the Finnish and Norwegian pastures are used during different seasons, causing differences in reindeer grazing history, and with time differences in vegetation. Additionally, local topography also impacts the vegetation composition and structure creating variation in local vegetation patterns. My research questions are: How vegetation patterns differ between summer- and winter- grazed areas, and which plant functional groups have the most significant difference? How local topography affects vegetation patterns, and does the effect of topography differ between summer and winter pastures? The data was collected from five 400 m long transects that crossed the fence and had vegetation plots with 10-m intervals. The %-cover and height of each vascular plant, bryophyte, and lichen species were estimated from 0.25 m ² plots. Later, species data was grouped into functional groups and general linear models were used to analyze differences in cover, height, species number, biomass, and leaf-area indices between countries. Topography indices were calculated in GIS for each plot and analyzed with random forest models to find out the most important topography indices explaining vegetation patterns. The vegetation data was collected by four teams, and therefore, the comparability in the collected data between teams was analyzed. Significant vegetation differences were found in the ground layer, with higher cover and biomass of bryophytes on the Finnish side (mean biomass 168.2 vs. 65.2 g m ⁻²). Reindeer lichens were more abundant on the Norwegian side (mean biomass 197.0 vs. 2.9 g m ⁻²) which is visible in aerial and satellite images and in the field. Among vascular plants, evergreen dwarf shrubs had higher biomass and leaf area index on the Finnish side and dwarf birch had higher cover and height on the Norwegian side. Topography indices had a higher level of variance explained on the Norwegian side, and higher at the ground layer compared to vascular plants. Elevation had the greatest impact on vegetation, and after that, topography protection index for 50 m and depth to water stream network for 2 and 10 ha. The differences between data collectors were not considered to have a major impact on the results. The results indicate that there are significant differences in vegetation between summer- and winter-grazed areas, mainly in the ground layer, and most differences are caused by differences in reindeer grazing history, but also local topography has an impact.		
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Tiivistelmä - Referat – Abstract <p>Tundravegetationen i forskningsområdet Jauristunturit påverkas starkt av ren-staketet som byggdes längs gränsen mellan Finland och Norge på 1950 talet för att förhindra sommarrenbetet på den norska sidan. Staterna använder sina betesmarken i forskningsområdet vid olika årstider, vilket orsakat olika stort betes tryck på de olika sidorna, och med tiden har det lett till stora skillnader i växtligheten. Dessutom har topografin också en inverkan, och kan skapa lokala skillnader i vegetations mönstren.</p> <p>Mina forskningsfrågor är följande: Hur skiljer sig vegetationsmönstren mellan sommar- och vinterbetesmarkerna, och vilka funktionella grupper uppvisar största skillnaden? Hur påverkar den lokala topografin på vegetationsmönstren, och finns det skillnader i påverkan mellan sommar- och vinterbetesmarkerna? Datainsamlingen gjordes över fem 400 m långa linjer som korsade ren-staketet, och hade växtrutor med 10 m mellanrum. Den procentuella täckningen och höjden av alla kärlväxter, moss- och lavararter estimerades från de 0.25 m² stora växtrutorna. Växterna delades in i sina funktionella grupper, och allmänna linjära modeller utfördes för att få skillnaderna i täckning, höjd, biomassa och löv-area indexen mellan länderna. Topografiindex räknades ut med GIS för varje växtruta, och analyserades med random forest modeller för att se vad i topografin som påverkar växtligheten mest. Funktionaliteten av vår datainsamlingsmetod analyserades också eftersom flera olika personer deltog i arbetet.</p> <p>Signifikanta skillnader mellan länderna hittades i markskiktet, med mera mossor på den finska sidan (biomassamedeltal 168.2 mot 65.2 g m⁻²), och mera renlav på den norska sidan (biomassamedeltal 197.0 mot 2.9 g m⁻²), vilket man även kan se i flyg och satellitbilder och i fält. Kärlväxterna uppvisade signifikant skillnad med mera vintergröna dvärgbuskarna på den finska sidan, och mera dvärgbjörk på den norska. Den lokala topografin förklarade en större del av vegetationsförändringarna på den norska sidan än den finska, och med en större inverkan på markskiktet än kärlväxterna. Den största inverkan på växtligheten hade höjden över havet, där efter kom index för topografiskt skydd för 50 m och distansen till vattennätverken för 2 och 10 ha. Skillnader mellan växt data insamlarna anses inte ha påverkat resultaten anmärkningsvärt. På basis av resultaten kan jag dra slutsatsen att skillnaden i växtlighet mellan sommar- och vinterbetesmarkerna är stora, i synnerhet i markskiktet, och det är till största delen orsakat av renbetet men också topografin har en påverkan.</p>		
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Abbreviations

BM	Biomass (g m^{-2})
C	Cover
Dtw 05ha	Depth to water stream network within minimum of 0.5 ha
Dtw10ha	Depth to water stream network within minimum of 10 ha
Dtw2ha	Depth to water stream network within minimum of 2 ha
Elev	Elevation
H	Height
LAI	Leaf Area Index
Mpi50	Morphometric protection index 50m
Sr	Solar radiation
Tpi10	Topography position index 10 m
Tpi50	Topography position index 50m
Twi	Topography wetness index
Vrm 3	Vector ruggedness measure with 3x3 m circular neighbourhood
Vrm15	Vector ruggedness measure with 15x15 m circular neighbourhood

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1 Introduction

Grazing of semi-domesticated reindeer (*Rangifer tarandus ssp. tarandus*) is an important form of land use in the northern Eurasia (Forbes & Kumpula 2009). Reindeer are abundant in all Arctic regions, and they provide important ecosystem services to local and indigenous people (Bernes et al. 2015).

Reindeer grazing can cause changes in plant communities, but also in ecosystem processes (Gurevitch et al. 2002). In heavily grazed areas, the long term-effects of reindeer grazing and trampling can be seen in changes in vegetation patterns (Bernes et al. 2015; Den Herder et al. 2003), mainly with reindeer lichens disappearing (Kumpula et al. 2014).

In the northern Fennoscandia, reindeer fences are widely used to keep reindeer in their herding districts, and to separate grazing grounds from each other. As the grazing pressure typically differs between the herding districts, vegetation patterns can be strikingly dissimilar on different sides of a reindeer fence (Kumpula 2006). Furthermore, local vegetation composition depends on several environmental and topographical gradients as well, e.g. elevation, slope, wetness, and solar radiation, to name a few. Therefore, variation along these gradients should be considered when studying vegetation changes in relation to grazing (Walker 2002).

Vegetation changes due to reindeer grazing, especially the effect on reindeer lichens, have been studied in many areas (Kumpula et al 2014; van der Wal 2006; Suominen & Olofsson 2000), but studies including both factors, reindeer grazing and topography, are less common.

The aim of the study is to examine vegetation patterns in the Jauristunturit study area, on both sides of the reindeer fence that follow the border between Finland and Norway, and to explain how differences in reindeer grazing history and local topography affect vegetation patterns.

2 Tundra vegetation, reindeer, and the effect of grazing and topography

2.1 Main patterns of tundra vegetation

The arctic tundra is a nutrient-poor habitat with extreme climatic conditions (Virtanen et al. 2016), which makes it a challenging environment for plants to grow. The plants in the arctic are highly adapted to this harsh environment, and they are often low growing due to the wind and the long snow cover.

The ground cover in the Fennoscandian continental tundra is covered with lichens and bryophytes, with some bare soil, stones, and litter. Lichens and bryophytes can grow on a shallow soil layer and are highly adapted to tundra climate. Both evergreen and deciduous dwarf shrubs are common, dwarf birch (*Betula nana*) being one of the few taller shrub species found on tundra heaths. The lower altitudes are occupied by mixed taiga and pine and birch woodlands (Oksanen & Virtanen, 1995).

Today, vegetation in the northernmost Fennoscandia is heavily influenced by reindeer grazing and trampling due to intensive reindeer husbandry (Den Herder et al. 2003; Adler et al. 2001; Egelkraut et al. 2020). This area is located in the northern boreal and tundra vegetation zones (Kumpula 2006; Bernes et al. 2015), and due to the cold climate, vegetation may be sensitive to disturbances and recover slowly from them. However, reindeer have been a part of the Fennoscandian tundra ecosystem since the last ice age (Suominen & Olofsson 2000) and have modified tundra vegetation since then (Johansen et al. 2019). For that reason, the plant species found in the tundra might be more resilient to disturbances, which could help them to recover faster when the grazing pressure is reduced (Moen & Danell 2003). Some plant species are also able to compensate after being grazed that might be an advantage over other plant species in the area (Järemo et al. 2001), but on the pastures with the highest grazing pressure, only a few species can survive (Helle & Aspi, 1983).

2.2 The northern Eurasian reindeer

2.2.1 Diet and behaviour

The northern Eurasian reindeer (*Rangifer tarandus ssp. tarandus*) are mostly domesticated or semi-domesticated, while there are large numbers in North America that are wild (Bernes et al. 2015). The North American reindeer are referred

to as caribou (*R. tarandus ssp. caribou*) (Bernes et al. 2015; Suominen & Olsson, 2000). Here I am going to focus on the Eurasian reindeer.

Reindeer are well adapted to the tundra (van der Wal 2006) with their highly adapted physiology, and their ability to digest a high variety of plant species, that are inedible for most other mammals. There are 106 plant species that have been found to be the most important for them, including 13 lichens that make up over half of the grazed food during a year (Nieminen et al. 1989).

Reindeer rely on lichens as their main food source in winter, but some evergreen plants are also important (Nieminen et al. 1989). In summer, on the other hand, they mainly feed on vascular plants, such as graminoids, forbs and leaves of shrubs (Bernes et al. 2015). During the long and harsh arctic winters, there can be periods when food is unavailable due to e.g., icing events or deep snow cover (Forbes et al. 2016). Therefore, it is of utmost important that reindeer gain enough weight during summer to survive the winters (Bernes et al. 2015).

Lichens are very sensitive to trampling, especially dry lichens in the summer break easily when tramped (Cooper et al. 2001); therefore, reindeer trampling in summer pastures may cause serious lichen damage (Den Herder et al. 2003). If the same pasture is used in winter, reindeer have troubles finding food, since their main winter food source is damaged, and its abundance decreased.

Reindeer select their habitat based on forage quality and quantity, especially in the beginning of the growing season when vegetation has higher heterogeneity (Iversen et al. 2014). In heterogeneous environments, large herbivores tend to choose forage from more nutrient-rich locations, and they can remember which locations and even patches that have already been consumed (Bailey et al. 1996). The distance to a water source and the slope incline is also both factors that affect the reindeer grazing patterns and vegetation (Bailey et al. 1996). Depending on grazing and vegetation patterns, grazing can lead to either increased or decreased vegetation heterogeneity (Adler et al. 2001).

On a plant species scale, reindeer grazing behaviour can be seen in preference to certain species, by selectively browsing and limiting their consumption to young leaves, shoots, and flowers of willows, if possible (Gurevitch et al. 2002). The timing when grazing occurs in relation to the plant's life cycle is also of importance because seed production may be harmed if grazing occurs before or during flowering (Gurevitch et al. 2002).

When forage is limited, reindeer must consume forage of lower quality (Bailey et al. 1996) and move over larger areas to find it (Iversen et al. 2014). More movement and lower forage quality could be a sign of a more homogenized forage availability for reindeer (Iversen et al. 2014). Disturbances and weather changes also force reindeer to move around which increases trampling (Moen & Danell 2003). The snow conditions in winter can make it more difficult for reindeer to move, and they will stay on and along ridges and hills where the snow cover is the thinnest (Johansen et al. 2019; Kumpula et al. 2015). After a snow-rich winter with little movement reindeer have an increased movement in the summer (Kumpula et al. 2015).

2.2.2 Migrations and reindeer herding

It is natural for reindeer herds to move over the seasons, looking for good feeding grounds. They migrate between summer and winter pastures, but also move around between different grazing grounds within seasons (Bernes et al. 2015). The Swedish reindeer, for instance, spend summers in tundra and forest-tundra, and winters in boreal forests (Bernes et al. 2015), and reindeer in Finnmark (Norway) use the inland mountain pastures during the winter and migrate in spring towards the coast for summer pastures (Suominen & Olofsson 2000).

Reindeer herding in Finland is notably different from reindeer herding in Norway and Sweden. In Finland, the reindeer herding area is divided into 57 fenced herding districts (Kumpula et al. 2015), and both indigenous and non-indigenous people are allowed to have reindeer (Suominen & Olofsson 2000). Every reindeer herding district has a cooperative of reindeer herders (*paliskunta*), and all reindeer within one district form a herd and are herded as one group (Suominen & Olofsson 2000). The reindeer never leave their district (due to reindeer fences), but they are herded between locations within it to reduce overexploitation (Suominen & Olofsson 2000). In Norway and Sweden, reindeer herding is restricted to the indigenous people alone, and they have their own stocks and herd them over large areas (Suominen & Olofsson 2000). The Norwegian side have fences within their reindeer herding areas to separate different seasonal pastures

from each other, and these were built in the mid-1980s (Evans 1996). The reindeer fences affect vegetation patterns due to differences in grazing pressures that can occur between the different sides.

The reindeer fence between Sweden and Norway, has caused changes in the natural migration routes, and now reindeer summer grazing occurs in sensitive mountain terrain, was previously used only during migrations (Moen & Danell 2003). Reindeer also tend to migrate along the fences, which often leads to increased erosion in a 100-200 m wide zone next to the fences, and the erosion closest to a fence is 1-3 mm every year due to trampling and harsh weather (Evans 1996).

Supplementary feeding has made it possible to have even bigger herds, and help the reindeer survive in areas with less food. Finnish reindeer gets supplementary feeding when needed, to maintain a high productivity level (Kumpula et al. 2015), and it is also provided in some parts of Northern Norway where the lichen cover has decreased (Johansen et al. 2019).

2.2.3 Effects of grazing on tundra vegetation

According to van der Wal (2006) tundra vegetation has three different stable states, dominated by lichens-, mosses- or grasses respectively. All these three conditions are resistant to disturbance, but if the pressure is too hard, they may shift to another condition (van der Wal 2006). A high grazing pressure over a long period of time, reduces lichen cover, exposes soil, and over time the species composition will change, and other species will take over (Johansen et al. 2019). When the pressure is decreased, the vegetation can shift back to the original state (van der Wal 2006). If the areas surrounding a previously disturbed area have great abundance of lichens, the lichen cover will be able to recover within a few years, given that the area is undisturbed, otherwise it will take longer (Johansen et al. 2019).

The grazing intensity also affect vegetation (Elmendorf et al. 2012). If an ecosystem has adapted to a certain grazing intensity level, anything other than that would cause a disturbance (Suominen & Olofsson 2000). Large herbivores, such as reindeer, can with increased grazing pressure force vegetation to a condition where the productivity of the ecosystem is higher, meaning from lichen- to

a moss-dominated state, and from moss-dominated further to grass-dominated state (van der Wal 2006). With a higher productivity, the carrying capacity of the ecosystem increases, but there are also other factors, like moisture, that can affect the carrying capacity (van der Wal 2006). Reindeer also affect the vegetation with their defecations, that alter the nutrient cycling and the overall nutrient composition of the soil in the area (Suominen & Olofsson 2000). Sundqvist et al. (2019) found that deciduous shrubs and lichens were lower in grazed areas, while evergreen shrubs, graminoids, and bryophytes benefited from grazing.

2.3 The effects of topography on tundra vegetation

In addition to grazing, vegetation is affected by topography, with abiotic and biotic factors varying with topography (Dearborn & Danby, 2020; Oksanen & Virtanen, 1995). Slope for instance, can create differences in water flow, solar radiation, and amount of wind exposure. The combined effect of these factors can lead to, for example, local differences in humidity and temperature (Alexander et al. 2016). The topographic position has also an effect, for instance, there are differences in vegetation and ecological processes in abiotic and biotic factors between a ridge and a valley (Alexander et al. 2016). Topography also affects winter snow conditions and creates local differences in snow cover thickness, which highly affects the thermal conditions in the ground (Niittynen et al. 2020). This causes local differences in the length of the growing season and affects small scale tundra vegetation patterns (Niittynen et al. 2020).

Previous research has shown that treelines are strongly determined by topographical and ecological processes in alpine regions (Dearborn & Danby, 2020). Local ice content in permafrost tundra is also affected by soil moisture and topographical position (Wang et al. 2019), and topography might also influence micro-climates and therefore vegetation (Eisenlohr et al. 2013; Wang et al. 2019). Räsänen et al. (2021) suggested that the importance of topography on vegetation patterns is dependent on the general landscape of the area, with topographic indices having a greater importance in certain landscapes.

Previous studies on vegetation differences in relation to reindeer grazing or topography differences have been conducted in the Northern Fennoscandia (e.g.,

Sundqvist et al. 2019; den Herden et al. 2003; Suominen & Olofsson 2000; Virtanen et al. 1999; Oksanen & Virtanen 1995), and some even in the same research area of this study. The inclusion of both topography and grazing differences is rare. The vegetation in Northern Fennoscandia varies between the coast and the inland, and between the boreal and arctic (Oksanen & Virtanen, 1995). There are also variations between lowland and summit, and in the topography between ridge and depression (Oksanen & Virtanen, 1995), which indicates that it might be important to account for both topography and grazing differences in this area.

3 Research questions

This study is part of a 4-year project CHARTER ("Drivers and Feedbacks of Changes in Arctic Terrestrial Biodiversity" <https://www.charter-arctic.org/>). CHARTER aims to develop better climate modelling tools that includes not only climate impacts but also the impact of local livelihoods and help inhabitants to better adapt to climatic and biodiversity changes. The goal of this study is to examine the role of reindeer grazing history and local topography in affecting vegetation patterns in summer-grazed (Finland) and winter-grazed (Norway). I will compare the cover (c), height (h), biomass (BM), and leaf area index (LAI) of different plant functional groups, lichens, bryophytes, and species diversity between countries. The research questions are:

- How vegetation patterns differ between summer- and winter-grazed areas and which plant functional groups have the most significant difference?
- How local topography affects vegetation patterns and does the effect of topography differ between summer- and winter-grazed areas?

The hypotheses are that there will be differences in vegetation between summer- and winter-grazed areas, especially in the ground layer, but probably also in other functional groups that are preferred forage for reindeer. It is expected that local topography will have an impact on the vegetation patterns, but it will most likely vary between functional groups. The overall topography impact is expected to be lower than the impact of grazing. The study transects were chosen

to have similar conditions on both sides of the fence, therefore the impact of topography is likely to be similar on both sides.

4 Materials and methods

4.1 The study area

The field data was collected in the Jauristunturit (Jávrresduotta) study area, in the Fennoscandian oroarctic tundra zone (Virtanen et al. 2016) between the 13-18th July 2020 (Figure 1). The area is both part of the Finnish Näkkälä and the Norwegian West Finnmark reindeer herding areas (Kumpula, 2006). The mean temperature in the area, for the years 1961-2019 is -2,55°C, with a decadal increase of 0.4°C, and the mean precipitation 424 mm with a decadal increase of 2.84 mm (Finnish Meteorological Institute, open data, described in Aalto et al. 2016). The terrain consists of open fells and heaths, with some small willow- and graminoid-dominated wetlands (Kitti et al. 2008; Kolari et al. 2019). Vegetation in heaths is a typical *Betula nana-Cladina* type of vegetation (Virtanen et al. 1999) (Figure 2). *Cladina* refers to reindeer lichens and it is a subgenus of the *Cladonia* group (McMullin & Rapai, 2020). This vegetation type is described as a lichen rich type that is often inhabited also by *Vaccinium myrtillus*, *Flavocetraria nivalis*, and *Phyllodoce Caerulea* (Virtanen et al. 1999).

Previous studies conducted in Jauristunturit study area are focused on socioeconomic factors, reindeer management, soils, wetlands, microbial ecology, and remote sensing (Kolari et al. 2019; Forbes et al. 2006).

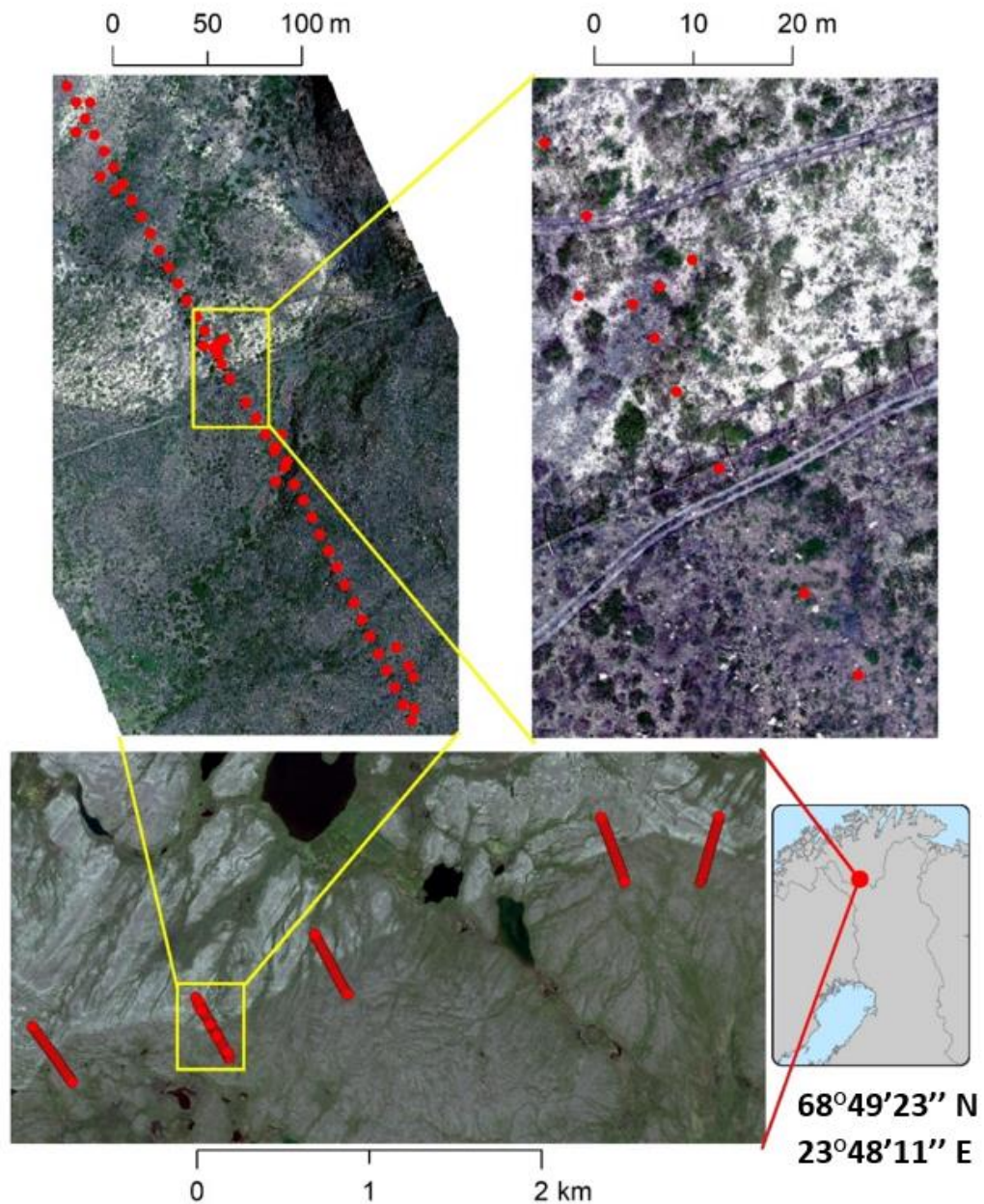


Figure 1: The location of the study area and the five transect lines (bottom panel), and a more detailed image of one of the transects (top panel). The top panel also includes the extra vegetation plots that were made for testing the method. Drone images (top panel) were acquired by Timo Kumpula and Pasi Korpelainen in 13-14.7.2020. Satellite image (bottom panel) is a WorldView-2 image taken on 23.8.2015 (©Digital Globe).

The reindeer fence between Finland and Norway was built in the mid-1950s, to prohibit reindeer from crossing the border (Figure 2). The fence has caused different grazing pressures on the different sides of the fence, leading to

land cover changes that are clearly visible in the field and satellite images (Kumpula 2006)(Figure 1). The Finnish side of the fence is absent of larger patches of lichens, whereas they exist on the Norwegian side, especially in the border area towards Finland (Johansen et al. 2019). The Norwegian pastures have only been used for winter grazing since the 3-m-high fence was built, and the Finnish side only for summer grazing (Kumpula 2006). An exception occurred in late 1970s to the mid-1990s when the Finnish side was used year around (Kumpula, 2006). Summer grazing on the Finnish side has led to extensive diminishing of the lichen cover, leading to reduced forage availability in winter, the season when reindeer mainly rely on lichens. Therefore, the Finnish side is nowadays used only in the summer. Snow cover protects lichens on the Norwegian side from extensive eating in winter and the forbidden summer grazing allows the lichens to grow in the summer without being trampled.

As the differences in grazing pressure, are caused by the reindeer fence along the national border, from now on, country refers to the differences in grazing history between the countries.

4.2 The fieldwork

The chosen method for this study was the use of transect lines, that were selected based upon their representation of a typical tundra heath vegetation, and that the transects had as equal conditions as possible on both sides of the fence. The fence creates an experimental study setup, with summer grazing in the Finnish side and winter-grazing in the Norwegian side.

Five transects crossed the national border and the reindeer fence in a 90-degree angle. The fence was always placed in the middle of the 400-m long transects (Figure 1), and vegetation plots were made with 10-m intervals. This added up to 20 vegetation plots on each side of the fence, 40 per transect, and 200 in total. The GPS locations were recorded for every plot, with TOPCON Real-Time Kinematic (RTK) positioning with a mean spatial accuracy of 1-2 cm. Every 4th plot was marked permanently for further research, and all plots were photographed (Figure 3).



Figure 2: A photograph of the reindeer fence and typical *Betula nana*- *Cladina* type vegetation in the Jauristunturit study area (Norwegian side) (Tarmo Virtanen 2020).

The vegetation plots were the size of 50 cm × 50 cm (Figure 3) and when inventoried, the person was always facing the fence. For every vegetation plot, we identified the species, visually estimated the percentage cover of each species (for the shrubs, we identified green and brown vegetation), litter, bare soil, and rocks, and measured the height of all vascular plants and reindeer lichens with a ruler (same technique as in Räsänen et al. 2019).

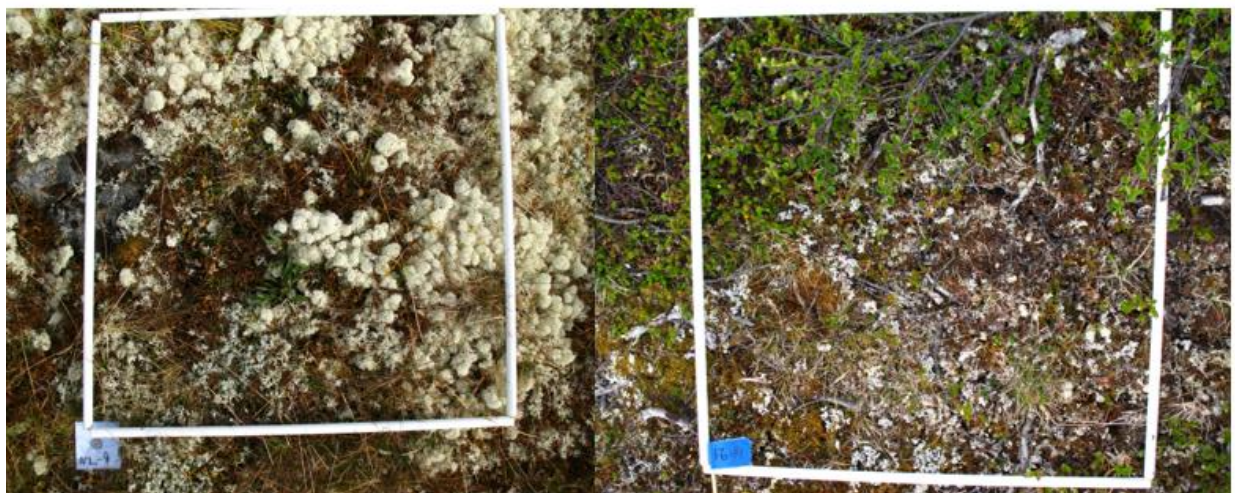


Figure 3: Pictures of vegetation plots (50cmx50cm) taken during the fieldwork. On the left side, one (permanently marked) vegetation plot from the Norwegian side and on the right side one from the Finnish side.

We did additional vegetation plots to test the comparability of the data collection between the four field work teams, because all teams have differences in field inventory experience. The species were identified and the %-coverage estimated. The plots were selected to present major vegetation communities in the study area. We chose 16 vegetation plots in total, 8 on both sides of the fence. All teams inventoried the same vegetation plots, and the data was compared to see if there was a significant difference in the data collected by different teams.

4.3 Plant functional groups

Plant species were divided into the following functional groups: vascular plants, evergreen dwarf shrubs, deciduous dwarf shrubs, dwarf birch (*Betula nana*), forbs and graminoids (grasses, rushes, and sedges), as well as reindeer lichens, other lichens, and bryophytes (Chapin et al. 1996) (species list in Appendix 1). The functional group of vascular plants consists of evergreen and deciduous dwarf shrubs, dwarf birch, forbs and graminoids. Grouping into functional groups was done due to interest in the broader differences between the countries, not in the species level.

In the data collection tests, the same functional groups were used, except for forbs and graminoids that were combined as one group, since the amount of both was low, and deciduous dwarf shrubs was combined with dwarf birch for the same reason.

4.4 Response variables calculated from the field data

Total number of species, heights (H), covers (C), biomass (BM; g m⁻²), and leaf-area index (LAI) were calculated for each functional group for each plot (Table 1). Covers were calculated by summing total coverage (green + brown) of the functional group in the plot and average heights were calculated by adding all the species heights in the plot times their coverage and dividing with total coverage.

Then BM and LAI were calculated based on allometric equations derived from ordinary least squares regressions (Table 1). The equations in a few cases produced negative values for BM and LAI, and these were manually set to zero. For vascular plants, BM and LAI were calculated as the sum of the values for the functional plant groups that belong to this group. LAI was calculated only for vascular plants. For the other lichens than reindeer lichens, BM was not calculated due to the lack of suitable equation.

Table 1: Table of equations used for the calculation of BM and LAI. The C stands for summed total cover and H for averaged height (Räsänen & Virtanen, unpublished data; Kumpula et al. 2014). Räsänen & Virtanen (unpublished data) is used for all equations except reindeer lichens while Kumpula et al. (2014) was used for the reindeer lichens equation. Similar equations were used also e.g., in Juutinen et al. (2017); Räsänen et al. (2019).

<i>Functional group</i>	<i>BM</i>	<i>LAI</i>
<i>Evergreen dwarf shrubs</i>	$= 6.633 + 2.527 * C$	$= 0.01701 + 0.00908 * C$
<i>Deciduous dwarf shrubs</i>	$= 0.929 + 2.964 * C$	$= -0.02006 + 0.0193 * C$
<i>Dwarf Birch (Betula nana)</i>	$= 5.0168 + 0.135 * C * H$	$= 0.00451 + 0.00777 * C$
<i>Forbs</i>	$= -0.171 + 0.0818 * C * H$	$= -1.886e-02 + 1.126e-03 * C * H$
<i>Graminoids</i>	$= 11.202 + 0.0505 * C * H$	$= 6.579e-02 + 3.853e-04 * C * H$
<i>Reindeer lichens</i>	$= 18.717 * ((H/100) * (C/4) / 10^4)^{1,3}$	Not applicable
<i>Bryophytes</i>	$= -3.900 + 7.503 * C$	Not applicable

I also counted the Shannon's diversity index for each plot, and this was done based on the coverage of each species. Shannon's diversity index is one of the most used in ecological studies, because it accounts for both the number of species and their abundance (Magurran 2004).

Several topography indices calculated for the vegetation plots, and the indices were chosen as the most relevant for this study (Table 2). These were calculated from Norwegian digital terrain model with 1-m spatial resolution and based on laser scanning data (Kartverket, 2020). The indices were compared with the vegetation groups to examine their possible effect on the vegetation.

Table 2: The topography indices used in this study, with their abbreviation, whole name, and definition.

Abbreviation	Name	Definition
<i>elev</i>	<i>Elevation</i>	Height above sea level in meter.

<i>slope</i>	<i>Slope</i>	Slope steepness in percent.
<i>Mpi50</i>	<i>Morphometric protection index 50m</i>	Analyses how well the specific location is protected based on 50 m neighbourhood radius (Yokoyama et al. 2002).
<i>Sr</i>	<i>Solar radiation</i>	Amount of annual solar radiation during May-September, calculated with two-hour intervals during six days with 30-day intervals (Boehner et al. 2009).
<i>Twi</i>	<i>Topography wetness index</i>	Models the wetness of the location based on upslope contributing area and local slope (Boehner et al. 2006).
<i>Tpi10</i> <i>Tpi50</i>	<i>Topographic position index for 10 m and 50 m neighbourhood radiuses</i>	Describes the relative altitudinal position of a location in relation to the surrounding landscape (Guisan et al. 1999; Alexander et al. 2016).
<i>Vrm3</i> <i>Vrm 15</i>	<i>Vector ruggedness measure with both 3x3m and 15x15m circular neighbourhood</i>	Examines local variations in the surface of the terrain by measuring vector dispersion (Sappington et al. 2007).
<i>Dtw_05ha</i> <i>Dtw_2ha</i> <i>Dtw_10ha</i>	<i>Depth to water with stream network within minimum of 0.5 ha, 2 ha and 10 ha catchment area</i>	A moisture index modelling water table depth, calculated based on elevation and modelled stream network (Murphy et al. 2007).

4.5 Statistical analyses

The statistical analyses were conducted in RStudio (Version 1.4.1106) and SPSS (Version 27). Random forest models and the data collection testing were made in RStudio, and vegetation analyses were made in SPSS. A logarithmic transformation ($\text{LOG}(1+x)$) was used for some variables because the assumptions of normal distributions were not met (Table 3).

The functional plant and lichens groups and their C, H, BM, and LAI data were checked for normal distribution, and equal variances were estimated based on the outcome of Levene's test. General linear models were then performed to compare the vegetation between the two countries. Country was used as a fixed factor in the models, to evaluate if there was difference in functional plant groups between countries. To minimize the possible difference between transects, transect was used as random factor.

The topography indices (Table 2) were analysed with random forest regressions (Breiman 2001) with the randomForest-package (Liaw & Wiener, 2002) in RStudio software, to examine how much of the differences in vegetation can be explained by topographic indices. The test is based on an ensemble of decision trees forming a forest, and when taking the average prediction of each tree we get the random forest output. This gives a higher accuracy than the use of only one tree. The out-put value explains how much of the variance is explained by the explanatory variables, in this case, topography indices. Random forest models also rank the explanatory variables based on their importance. The tests were carried out for each functional group and their C, H, BM, and LAI, and the explanatory variables were ranked by their importance. This was done both for original values and the logarithmically transformed values. The Random forest regressions were carried out for the Finnish and Norwegian data separately, both with and without the transect line as a factor, and for the whole dataset, both with and without the country and transect as factors. Scatter plots were done in RStudio.

For the data collection testing, the %-cover estimates were compared, and the number of species were compared between teams. This was done in RStudio with one-way ANOVA tests, with team as a fixed factor and the functional groups as variables. The normal distribution was estimated by visual estimations of histograms, and log-transformation was used for coverages of all functional groups, because the assumptions of normal distribution were not met, except for the vascular plant's coverage. Equal variances were estimated based on the outcome of Levene's test.

A correlation plot was made in RStudio software with the corrplot package (Wei et al. 2017) to examine the amount of correlation between explanatory and dependent variables. The Shannon's diversity index calculations were conducted in RStudio software with the package *vegan* (Oksanen et al. 2019).

5 Results

5.1 Correlations between vegetation and topography variables

No strong correlations within the vegetation data and the topography index data were found (Figure 4). The correlation between C, H, BM, and LAI within the same functional group was to be expected because C and H are used for the calculations of BM and LAI.

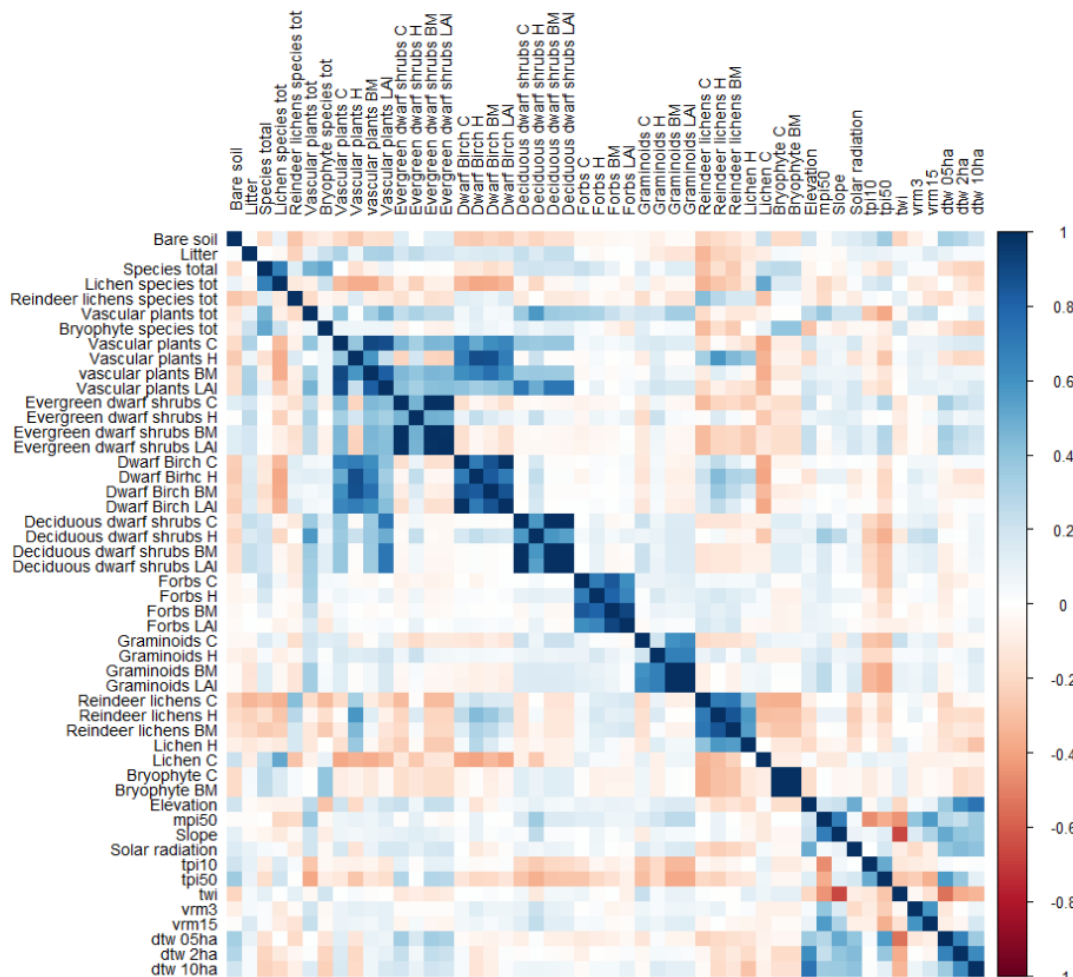


Figure 4: Correlation plot of the vegetation data and the topography indices. The dark blue (1) indicates that there is a correlation, and dark red (-1) indicates that there is a negative correlation, and white (0) indicates no correlation between the variables.

5.2 Vegetation patterns and the fence

There were no significant differences in graminoids, forbs, deciduous dwarf shrubs, and bare soil between countries (Table 3). For vascular plants, only H showed significant difference between countries, with Norway having significantly higher vascular plants. Dwarf birch H and BM showed a similar trend, with higher

values in Norway. For evergreen dwarf shrubs, BM and LAI showed significant differences, with higher values in Finland compared to Norway.

For the ground layer functional groups (i.e., lichens and bryophytes), significant difference was found in reindeer lichens in each test (i.e., C, H and BM) with considerably higher values in Norway than in Finland (Table 3). The other lichens did not show any significant difference, but all lichens in total showed significant difference between countries in C and H, with Norway having higher values. Bryophytes on the other hand showed significant difference in C and BM values, with Finland having higher values. The coverage of litter was significantly higher in the Finnish side.

On a species level, total amount of lichen species was not significantly different between the countries, but the amount of reindeer lichens species was significantly higher in Norway than in Finland, and for the other lichen species the trend was the opposite.

On average, the Shannon diversity index values were higher on the Finnish side, although the difference was small, with the mean values being 1.9, 1.7 in Finland and Norway, respectively.

To visualize the difference between the countries and the transects, bar plots were drawn of the average biomasses (Figure 5). Some transects had larger BM on one side of the fence than the other, and the amount differed also between transects. Vascular plants and reindeer lichens had the highest BM values, and the amount of reindeer lichens and bryophytes differed extensively between countries. We found only small amounts of forbs, and on the Finnish side only in one transect, therefore forbs have low values.

Table 3: The results from the general linear models, and the mean and standard deviation (in parenthesis) calculated for each country. Statistically significant p-values (≤ 0.05) are marked with bold. Cover values are in %, heights in cm, and BM in (g m^{-2}).

Species	FIN	NOR	F	p	Note
<i>Reindeer lichens</i>					
cover	5.071 (6.028)	35.69 (29.27)	40.63	0.003	log
height	1.120 (0.662)	3.527 (2.767)	51.44	0.002	log
BM	2.884 (6.536)	197.0 (358.3)	60.28	0.001	log
Species total	1.95 (0.796)	2.41 (0.753)	8.690	0.042	

Vascular plants

cover	44.72 (23.47)	40.01 (23.04)	3.546	0.133	log
height	7.063 (4.459)	9.060 (5.970)	11.37	0.028	log
BM	459.2 (269.2)	416.4 (280.7)	3.525	0.134	log
LAI	0.4410 (0.205)	0.3830 (0.235)	2.249	0.208	log
Species total	4.81 (1.293)	4.47 (1.617)	0.812	0.418	

Evergreen dwarf shrubs

cover	16.02 (13.35)	11.65 (15.47)	12.35	0.024	log
height	3.577 (1.982)	3.377 (2.277)	1.066	0.360	log
BM	188.2 (135.3)	142.4 (157.9)	14.05	0.020	
LAI	0.1490 (0.104)	0.1151 (0.133)	9.841	0.035	

Deciduous dwarf shrubs

cover	7.014 (8.223)	4.199 (8.961)	5.713	0.075	log
height	3.369 (3.139)	2.555 (3.648)	1.430	0.298	
BM	85.64 (98.55)	51.56 (107.2)	2.209	0.211	
LAI	0.1210 (0.153)	0.0714 (0.165)	3.314	0.143	log

Graminoids

cover	5.163 (6.409)	3.245 (4.075)	3.116	0.152	log
height	5.320 (3.330)	6.339 (4.042)	2.300	0.204	
BM	45.85 (18.71)	43.63 (20.11)	1.526	0.284	
LAI	0.0690 (0.028)	0.0663 (0.032)	1.362	0.308	

Herbaceous

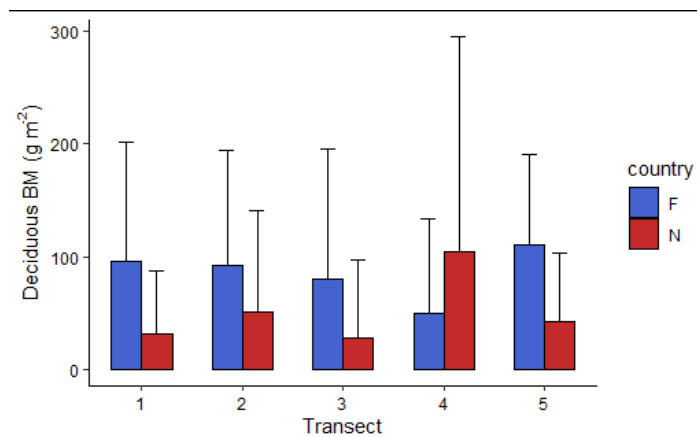
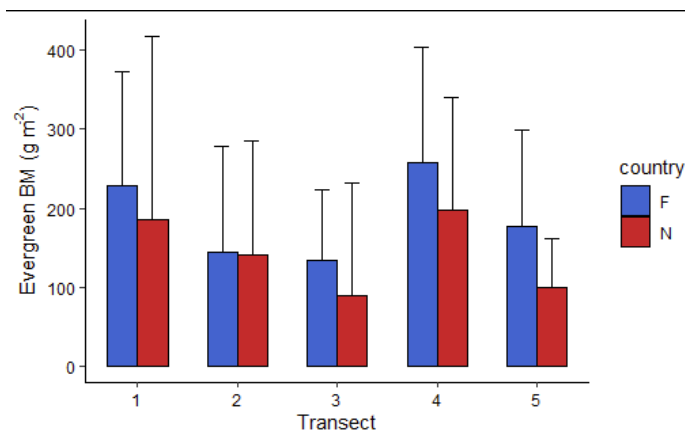
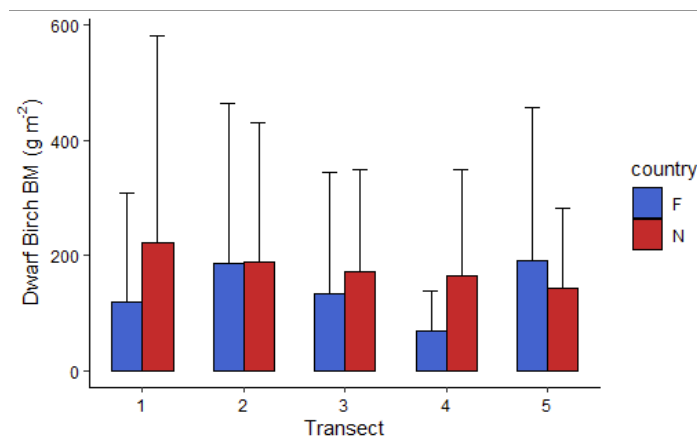
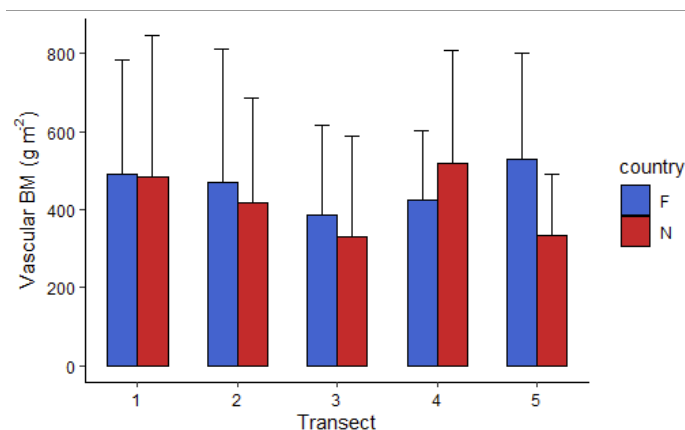
cover	0.193 (1.134)	0.457 (1.466)	0.572	0.492	
height	0.0660 (0.406)	0.4649 (1.439)	2.362	0.199	
BM	0.1271 (1.439)	0.4847 (2.189)	1.044	0.365	
LAI	0.00015 (0.0015)	0.000664 (0.005)	0.655	0.464	

Dwarf Birch

cover	16.33 (19.12)	20.46 (18.32)	4.733	0.095	
height	8.030 (7.205)	9.905 (7.757)	86.00	0.001	log
BM	139.4 (216.4)	178.3 (230.4)	50.72	0.002	log
LAI	0.1018 (0.120)	0.1295 (0.111)	3.150	0.151	log

Bryophytes

cover	22.93 (17.22)	9.134 (10.70)	54.86	0.002	log
BM	168.2 (129.2)	65.25 (79.79)	42.42	0.003	log
<i>Other lichens</i>					
cover	21.89 (15.47)	18.42 (18.06)	5.705	0.075	log
height	0.5617 (0.674)	1.487 (2.348)	6.240	0.067	
Species total	5.75 (2.027)	4.61 (2.035)	13.02	0.023	
<i>All lichens</i>					
cover	26.96 (15.59)	54.11 (26.68)	65.64	0.001	
height	0.2487 (0.121)	0.4738 (0.246)	43.53	0.003	log
Species total	7.70 (2.139)	7.02 (2.150)	5.479	0.079	
<i>Litter cover</i>	27.29 (21.10)	16.53 (14.47)	18.54	0.013	
<i>Bare soil cover</i>	2.330 (4.459)	1.111 (3.287)	5.997	0.071	
<i>All species total</i>	14.26 (2.557)	13.06 (2.655)	4.553	0.100	
<i>Shannon index</i>	1.914 (0.298)	1.733 (0.399)	10.90	0.030	



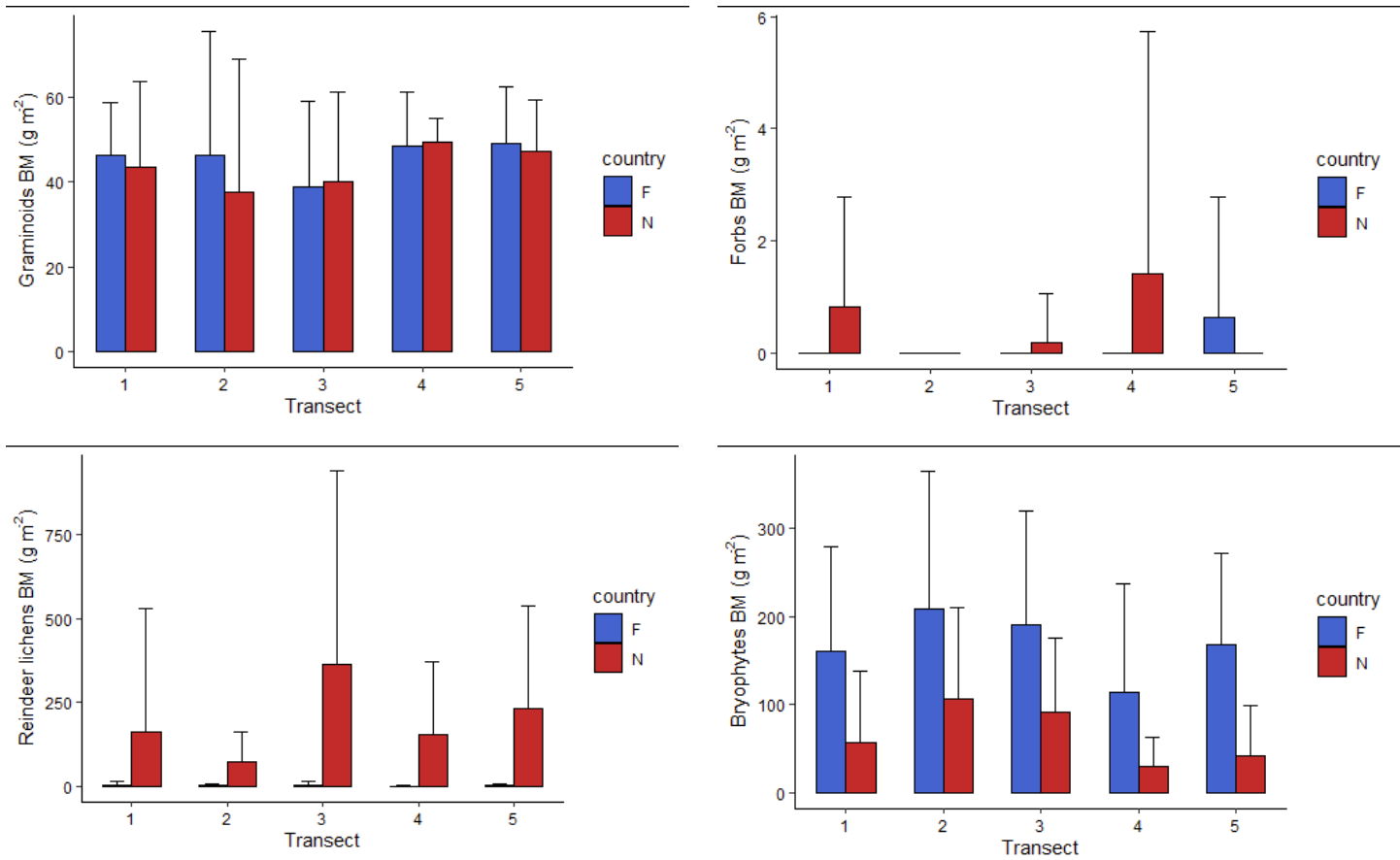


Figure 5: Average biomasses (g m⁻²), and their standard deviation per transect and country, for vascular plants, all its subgroups, bryophytes, and reindeer lichens. Due to the lack of BM estimations for other lichens than reindeer lichens, those are not visualised here. The Finnish side is in blue and the Norwegian in red. Note the different scale on y-axis.

5.3 Vegetation composition explained by topography indices

The random forest models on the logarithmically transformed dataset for both countries together, when country and transect line were included as factors, it yielded the highest level of explained variance. Only the results from tests where the explained variance was $\geq 15\%$ are presented. The tests were also conducted separately for the Finland and Norway, and the results are included to visualize the difference in explained variance between countries. The variance explanation level might be lower than 15%, and their explanatory variables importance levels were not examined.

The models for the whole data, in which at least 15% of variance were explained, comprised of vascular plants H, deciduous dwarf shrubs C, H, and BM, graminoids C, and LAI, reindeer lichens C, H, and BM, bryophyte C and BM.

For deciduous dwarf shrubs H, graminoids LAI, reindeer lichens C and H the non-logarithmically transformed dependent variable also gave significant results, but the explained variance was lower than for the logarithmically transformed dependent variable.

Here I focus only on the results of vascular plants, reindeer lichens and bryophytes. For the vascular plants H, TPI50, is the most important explanatory variable, with elevation being the second most important, and VRM15 as the third, and after that the DTW with stream network within minimum of 10, 2 and 0.5 ha, catchment areas (Figure 6). The level of variance explained was higher in the Norwegian (23.53%) than in the Finnish model (11.27%).

The topography indices that explained reindeer lichens C, H and BM the most are country, TPI50, elevation, and after that the DTW with stream network within minimum of 10, 2 and 0.5 ha, catchment areas. In all reindeer lichens tests, the Norwegian model had higher variance explanation percentages than the Finnish model. Reindeer lichens BM model had the highest amount of explained variance of all tests (61.9%).

The situation was similar for bryophytes, with country being the most important topography index, and elevation being the second most important. DTW was third most important with 2 ha minimum catchment area for bryophyte C and 10 ha for BM (Figure 6). The bryophytes variance explanation percentage has a negative value on the Finnish side for both C and BM, and therefore the Norwegian model also had higher degree of variance explained.

Scatter plot visualizations of the functional groups that exceeded the 15 % explanation rate and their most important topography indices show the trend directions (Figure 7, Appendix 2). The impact of country is comprehensively reported in the vegetation study results, and therefore not visualized here. The sample size was small, but the height of vascular plants was higher at lower elevations. The H, C, and BM of reindeer lichens also increased at lower elevations, as did C and BM of bryophytes. Vascular plants (Figure 7), and reindeer lichens showed to prefer average TPI50 values, and bryophytes prefer low DTW 2 ha values.

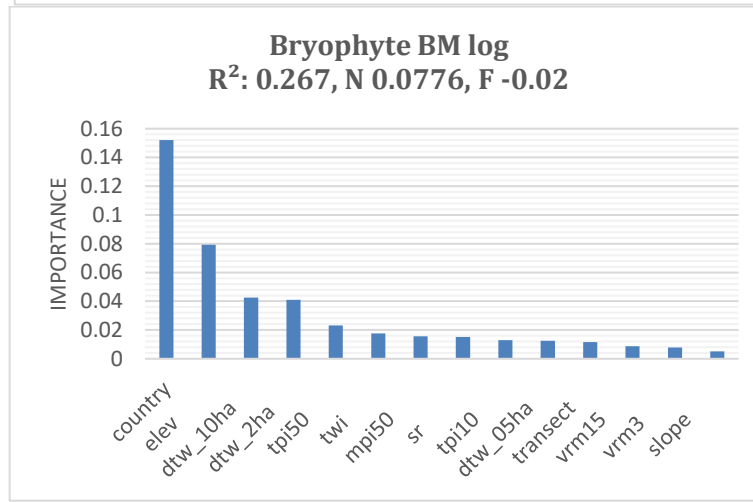
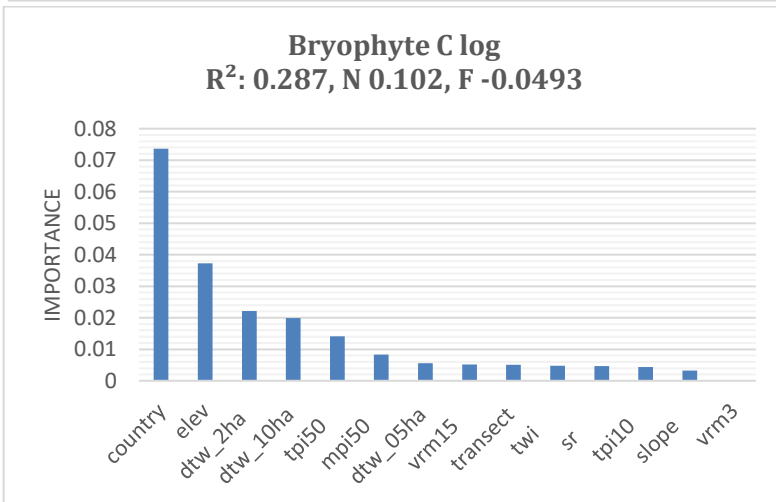
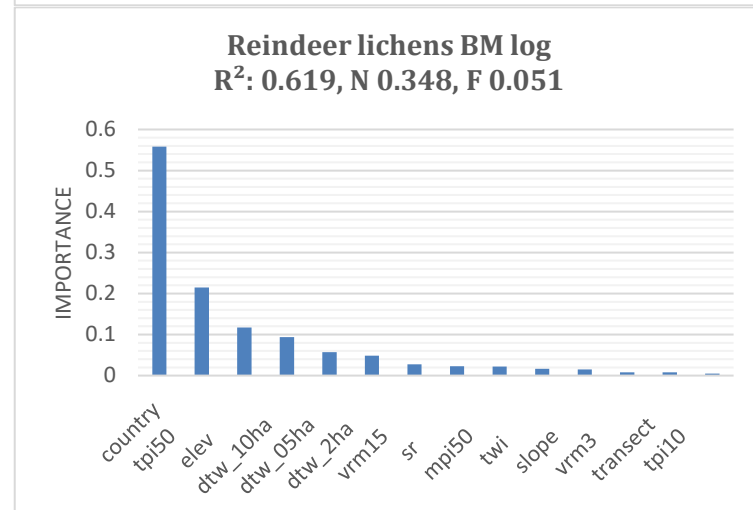
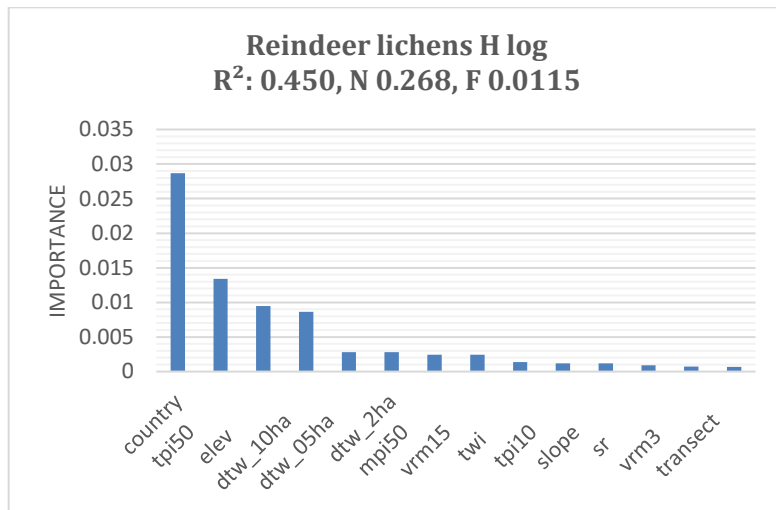
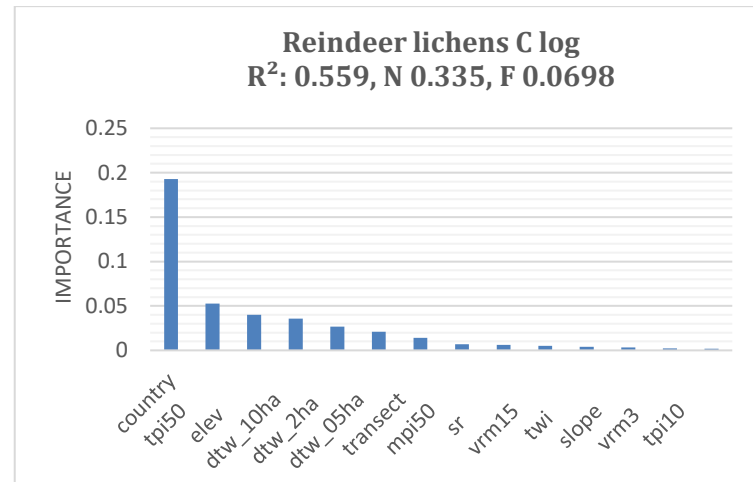
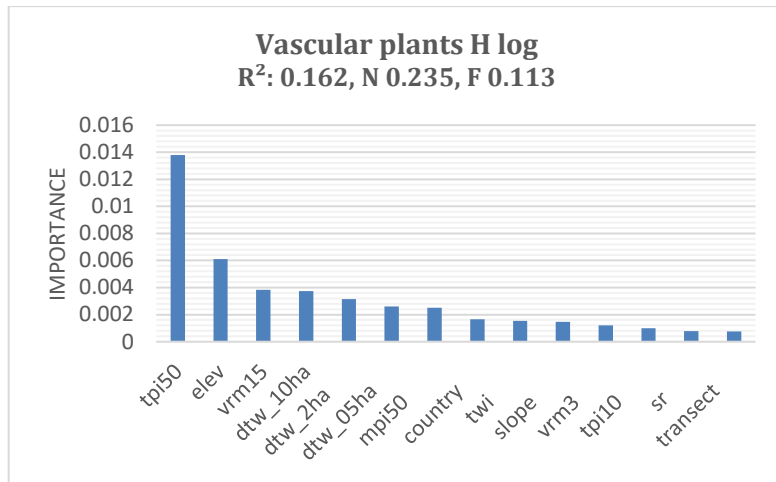


Figure 6: The results from random forest tests, with the explained variance (R^2) for the whole dataset as first, for Norway as second, and for Finland as third. The topography indices are organized by importance. Mind the scale.

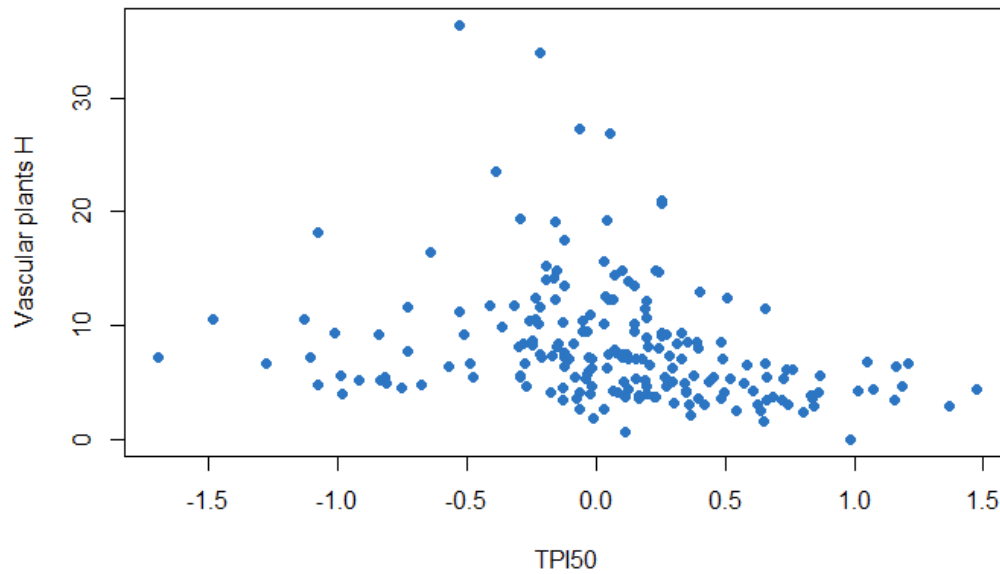


Figure 7: Vascular plant height and its most important topography index, topographic position index for 50 m.

5.4 Data collection testing results

The ANOVA test showed that the measurements differed significantly between teams in the number of vascular plants, bryophytes, forbs and graminoid species (Table 4). No significant difference was detected between teams when it came to the estimation of coverage, except for bryophytes.

Table 4: Data collection testing results, with mean and standard deviation (in parenthesis) for the teams, and F and p values from the ANOVA test. The logarithmic transformation is mentioned in notes. Total stands for the species in total. 0.05 as significance level for the p-value, and the significant values are in bold.

Species	Team 1	Team 2	Team 3	Team 4	F	p	Note
<i>Vascular plants</i>							
cover	40.03 (33.69)	39.72 (32.20)	65.43 (43.57)	33.85 (24.49)	2.713	0.0528	
species total	4.500 (1.033)	3.250 (1.571)	4.125 (1.088)	4.438 (0.964)	3.76	0.0153	
<i>Reindeer lichens</i>							
cover	18.76 (34.36)	16.69 (30.74)	19.21 (36.29)	18.84 (35.61)	0.062	0.98	log
species total	1.188 (1.047)	0.875 (0.885)	1.125 (1.025)	1.063 (0.998)	0.297	0.827	
<i>Evergreen dwarf shrubs</i>							
cover	13.77 (24.50)	13.02 (22.56)	16.82 (33.39)	11.60 (20.29)	0.037	0.99	log
species total	1.188 (0.544)	0.938 (0.772)	0.813 (0.750)	1.125 (0.500)	1.112	0.351	

Deciduous dwarf shrubs

<i>cover</i>	18.88 (22.62)	18.13 (27.33)	29.63 (35.69)	13.84 (17.68)	0.626	0.601	log
<i>species total</i>	1.438 (0.727)	1.313 (0.602)	1.438 (0.727)	1.438 (0.727)	0.128	0.943	

Herbaceous & graminoids

<i>cover</i>	7.381 (11.14)	8.575 (12.42)	18.98 (31.85)	8.413 (16.82)	0.73	0.538	log
<i>species total</i>	1.875 (0.719)	1.00 (1.095)	1.875 (0.957)	1.875 (1.088)	3.21	0.0293	

Other lichens

<i>cover</i>	23.16 (21.02)	21.64 (19.223)	25.52 (27.65)	21.33 (23.55)	0.193	0.901	log
<i>species total</i>	4.250 (2.082)	2.313 (2.414)	3.125 (1.668)	3.063 (2.0156)	2.401	0.0766	

Bryophytes

<i>cover</i>	23.56 (23.61)	10.31 (15.84)	15.70 (23.65)	10.73 (23.45)	3.483	0.0212	log
<i>species total</i>	2.250 (1.065)	1.125 (1.025)	1.500 (1.033)	1.063 (1.482)	3.5	0.0208	

6 Discussion

The results indicate that the vegetation in the study area is affected by reindeer grazing and topography, and that they have different effects on different functional groups. I expected differences in vegetation between summer- and winter-grazed areas, especially in the ground layer, but probably also in other functional groups that are preferred forage for reindeer. The ground layer had significant differences, and the impacts of reindeer grazing could be seen also in other functional groups. This is in line with the hypothesis of different grazing history, but not when it comes to topography. My hypothesis was that topography would have the same effect on the vegetation in both countries, but the results showed that topography had larger impact on the Norwegian side. The overall topography impact was expected to be lower than the impact of grazing, and this part of the hypothesis is in line with the results.

However, the different sides of the fence may be in different stable conditions due to the different grazing pressures (van der Wal 2006). The affect may be reversible, meaning that the vegetation could potentially recover when the grazing pressure is reduced or ceased, and transform into a previous stable state.

6.1 Differences in vegetation between Norway and Finland

The differences in vegetation between countries was most noticeable in the ground layer, with BM of reindeer lichens and bryophytes having the greatest difference. This was not surprising since it was visible to the naked eye and can be explained based on the reindeer herding and grazing patterns. My results show that reindeer lichens were significantly more abundant on the Norwegian side. The reduced amount of reindeer lichens on the Finnish side might be worrying since lichens have many important roles in ecosystems. They help to prevent erosion, regulate water flow, can fixate nitrogen and carbon from the atmosphere, increase air quality and albedo, and serve as food and nesting materials for animals (Zedda & Rambold, 2015). Therefore, we should protect them, especially from reindeer under snow-free periods (Kumpula et al. 2014).

The Finnish side had more coverage of bryophytes than the Norwegian, and this follows Bernes et al. (2015) conclusion that bryophytes are not as sensitive to reindeer trampling, and they can in fact grow more freely without the dominant reindeer lichens (Suominen & Olofsson 2000).

The results showed that the Norwegian side had significantly higher vascular plants. This result is probably highly influenced by dwarf birch because it is the only vascular plant that had a significant difference in H between countries. Dwarf birch C and LAI did not differ between countries, but dwarf birches were significantly higher in Norway, and that is probably the reason for the Norwegian side also having more BM of dwarf birch than the Finnish side. Interestingly C, BM and LAI of vascular plants did not differ significantly between countries. This could either be due to a non-existent difference or due to the variation in the subgroups for vascular plants equalizing the possible variation between countries. The results for the vascular plant subgroups show no significant difference between countries for graminoids, herbaceous plants, deciduous dwarf shrubs and neither for bare soil. Previous research on the wetlands in the area found that willows (*Salix* spp.) decreased due to summer grazing (Kolari et al. 2019), and that sedges (graminoids) increased in summer grazed areas, probably due to the decrease in willows (Kitti et al. 2008). I did not find any significant difference between countries when it came to willows or graminoids, which indicates that there

might be a difference in vegetation changes in the heaths compared to the wetlands, and vegetation changes are most likely very different in different habitats (Vowles et al. 2017). The effect of grazing was found to be nonsignificant on some graminoid species by Bråthen & Oksanen (2001), and on all shrubs and graminoids by Bernes et al. (2015).

When examining the vascular plants subgroups, evergreen dwarf shrubs BM showed significantly higher biomass for the Finnish side. The higher dwarf birch BM on the Norwegian side probably equalizes the values on evergreen dwarf shrubs BM on the Finnish side, and therefore, no significant differences in vascular plants BM between the countries was found.

The results for litter showed significantly more litter on the Finnish side, and previous research have concluded that litter increases in grazed areas. This is probably due to warmer top layers of soils having a negative effect on vegetation (den Herden et al. 2003), and therefore, climate change also contributes to increasing litter in the tundra (Elmendorf et al. 2012).

The total amount of lichen species did not show a significant difference between the countries, but the type of lichen species differed. The Norwegian side had significantly more reindeer lichen species, and the Finnish side significantly more other lichen species. It is likely that the lack of dominant reindeer lichens on the Finnish side enables other lichen species to grow (Suominen & Olofsson 2000). The number of vascular plants did not differ significantly between countries, and the other functional groups were not analysed on a species level.

The effects on grazing on biodiversity was analysed with the Shannon index, and it showed a higher diversity on the Finnish side than the Norwegian. This aligns with some previous studies, showing that high grazing pressure increases the biodiversity level (Suominen & Olofsson 2000), but other research has concluded the opposite. Löffler & Pape (2008) found that heavily grazed areas had lower species number and coverages than areas with lower grazing pressure, although sample size in this study was low. Their results showed a decrease especially in the number of lichen species and lichen cover, which again aligns with my results. It seems that the effect of grazing on biodiversity is hard to predict, since it depends on many factors, and therefore varies a lot between habitats. In fact, it is hypothesized that species richness decreases in nutrient-poor habitats and increases in nutrient-rich habitats due to grazing (Proulx & Mazumder,

1998). In this study area, probably the lack of dominant reindeer lichens, that could prevent other plants and lichens from growing (Helle & Aspi, 1983; Oksanen & Virtanen, 1995), creates space for other plants to grow. Oksanen & Virtanen (1995) also concluded that heaths with less reindeer lichens due to grazing and trampling, tend to have higher diversity than the heaths where reindeer lichens are dominating. Forbs and graminoids are also found to benefit from grazing of lichens, because it gives them more space to grow (Suominen & Olofsson, 2000). Also, Löffler & Pape (2008) concluded that graminoids were most species abundant in areas with high grazing pressure.

According to Evans (1996) the vegetation closest to a fence (100-200 m) experience higher disturbance from reindeer trampling than further away since reindeer tend to travel along the fences. The transects in this study were 400 m long, with the fence in the middle, leading to the conclusion that all transects would be in a disturbed zone. I briefly looked into the possible effect of the fence on the vegetation in the transects and could not find any signs of it and did not take it into account in later analyses. In further research the use of longer transects could be useful, to see if there is a more disturbed zone also in this study area.

In the data collection testing results, total number of species varied between the teams for some of the plant groups. This is probably caused due to the very different backgrounds, levels of experience, and the possibility that the inventory teams did not document all species. We focused especially on lichens, which could be a sign why they did not differ significantly between teams. Vascular plants group consist of many functional groups summed together, which probably increases the actual difference between teams. Among subgroups, only herbaceous and graminoids (counted together), and bryophyte C and number of species varied between the inventory teams. Overall, the data collection seemed to work quite well in this study and is not thought to influence the results significantly.

6.2 Local topography impact on the vegetation

The topography influenced vegetation, and the variance explained was lower on the Finnish than the Norwegian side. A reason for this might be due to grazing having larger effect on the vegetation on the Finnish side than topography. The Norwegian side is used as a winter pasture, and therefore, the vegetation is highly

affected by the depth of the snow cover in the winter. In low snow cover reindeer have easier access to vegetation, e.g., lichens, and the snow cover in turn is dependent on the local topography.

In all the random forest models, topography position index for 50 m radius (tpi50), elevation and country were the most important topography indices. Depth to water stream work was also always quite highly ranked, as was vector ruggedness measure 15x15m circular neighbourhood. This would indicate that the surrounding vegetation and topography, height above sea level, grazing pressure, and the moisture affects the overall vegetation the most. Alexander et al. (2016) concluded that topography protection index (TPI) was a really good predictor of vegetation changes, but they also pointed out that the importance of indices relates to the other topography indices, and the importance ranking might be different with more indices included.

Vascular plant height was affected by topography position index for 50 m, indicating that the surrounding topography within 50 m affects the height of vascular plants. The explanation rate was higher at the Norwegian side than the Finnish side, which might be due to the earlier results that the Norwegian side have significantly higher vascular plants than the Finnish side. Elevation also affected the vascular plant height. Indeed, higher areas are most likely more affected by weather and wind, which makes it more difficult for vascular plants to grow in height.

Reindeer lichens were most affected by country, which most likely have to do with the different grazing pressures. Topography position index for 50 m is the second most important factor explaining the variances for reindeer lichens, and depth to water stream network for all three different sized areas followed. This indicates that reindeer lichens might be sensitive to the surrounding topography, and the moisture level it contains.

For bryophytes, country and elevation was the factors that most affected. For country, the reason most likely is the same as for reindeer lichens, but it affects mosses in the opposite way. Bryophytes have previously showed to increase in species richness with elevation, and lichens showed to decrease after their peak in 400 m above sea level (Bruun et al. 2006). The bryophyte overall model percentage values were low, and the negative values for the Finnish side

could indicate that other factors, such as grazing, has a more significant effect on the bryophytes and therefore, topography effects do not appear.

From the scatter plots a trend could be seen in the data, indicating that for vascular plants, reindeer lichens and bryophytes the conditions are in general better at lower elevation. Vascular plants and reindeer lichens showed to prefer average TPI50 values, indicating that they grow best in places in between highly exposed and highly protected areas in the landscape. DTW 2 ha indicates a semi dry area, and bryophytes preferred low DTW 2 ha values. This indicates that they prefer more humid spots in a dry area, they are therefore more likely to grow in depressed spots.

A previous study on treelines and topography in the subarctic alpine Canada by Dearborn & Danby (2020) showed that treelines facing different directions are affected and limited by different biotic and abiotic factors because they vary strongly with slope. They concluded that the north facing treelines are going to change more than the south facing ones, but climate change will most likely have an effect at landscape level. This indicates that topography not only affect the local vegetation patterns, as was visible in the results, but also at much larger scales.

There are some definite challenges when accounting for topographic factors in a study. Topographic scale can be divided into micro (Wang et al. 2019) and macro (Walker 2002), which are not always clearly defined and may thus differ between studies. Another challenge is what topographic indices are relevant to include. There is a myriad of different topographic indices that you can account for (Franklin 2020).

6.3 The impact of climate change

The differences in vegetation between the two countries are mainly caused by reindeer grazing, even though topography indices also contribute to the variations. Climate change also has an impact on the vegetation (Elmendorf et al. 2012), due to changes in the temperature and precipitation, that exposes the environment to even more stress (Chapin et al. 2005).

Ecosystems overall will respond to disturbances differently, depending on their current environmental state. This is because change is determined by the

ongoing temperature and moisture regimes (Cowles et al. 2018). Biotic, abiotic, and environmental factors also influence the size of change in ecosystems, and different plants e.g., might have adapted to different thermal optimum temperatures, and therefore responds differently to warming (Cowles et al. 2018). Even the individual species could be affected differently to the exact same disturbance (Elmendorf et al. 2012).

When discussing environmental disturbances, the changing climate is a considerable concern. Climate warming contributes to an increased mean height in vascular plants, especially deciduous shrubs, but also in evergreen, graminoids and forbs (Elmendorf et al. 2012). The results indicated that vascular plants height was more affected by topography than grazing pressure, which could contribute to their fast response to warming climate. Shrub expansion in the Arctic is known to be explained by increased summer warming (Berner et al. 2020; Elmendorf et al. 2012). Shrub covers affect the surrounding vegetation for example by decreasing the surface albedo, affecting the snowmelt, and via that affecting both soil moisture and temperature (Elmendorf et al. 2012; Cowles et al. 2018). With the shrub cover changing due to climate warming, the overall change in the ecosystem is increasing, but reindeer grazing has been shown to decrease the impact by inhibiting the growth of shrubs (Kitti et al. 2008; Kolari et al. 2019). This means that reindeer can potentially slow down shrub expansion, a phenomenon also called arctic greening (te Beest et al. 2016; Ravolainen et al. 2014), and this could slow down the ecosystem change.

Lichen growth rates are affected by the overall moisture gradient, including both precipitation and humidity, and with changes in precipitation due to climate change, we will probably see more changes in the lichen growth rates in the future (McMullin et al. 2020). Warming winters and increased summer precipitations affect lichens positively, while warming summers and increased snow cover in the winter affects them negatively (Kumpula et al. 2014). An overall decreased lichen cover affects both the moisture gradient and the temperature in the soil (den Herder et al. 2003). Soil development takes time in the tundra due to the cold climate, and in areas with thin soil layer, erosion can take place (Moen & Danell 2003). The vegetation protects the soil from erosion and increases the soil layer with litter (Moen & Danell 2003), but the increased temperatures might increase

the decomposition rates in the soil, which in turn might affect the whole vegetation and therefore also the animals living there.

The least amount of reindeer lichen BM was found in the pastures used in snow-free seasons, indicating that lichens are sensitive also to grazing and trampling (Kumpula et al. 2014). Snow cover protects lichens during winter, but during the snow free seasons the harm caused by reindeer trampling is substantial (Den Herder et al. 2003), and a reduced lichen cover and height, increases the temperature in the soils (Suominen & Olofsson 2000). I saw the harm of reindeer grazing and trampling in my research, with lower lichen BM at the Finnish side. Therefore, the vegetation and soil on the Finnish side probably already are affected by warmer temperatures in the summer, than the Norwegian side. The decreased cover of lichens on the Finnish side is caused by summer grazing, but the pastures are still being used for summer grazing which indicates that the area is not being overgrazed. Migrations between grazing grounds are important for grazing pressure to be distributed over larger areas and the sustainability of pastures maintained. The combined effect of grazing, trampling and climate change will most likely have large impacts on the vegetation in the future, especially on the sensitive lichens, which already can be seen (Maliniemi et al. 2018).

Climate change does not only cause a warming climate but also affects the length of the growing-season, due to a longer snow-free period, and seasonal precipitation patterns (Elmendorf et al. 2012; Chapin et al. 2005). The results of the longer snow-free periods are already showing with warming of the arctic which are bound to amplify ecological changes in the future (Chapin et al. 2005). Increased precipitation and temperatures have both positive and negative effects on reindeer pastures (Johansen et al. 2019). The positive effects can be seen in higher temperatures increasing growth, especially for grass, herbs and heather, and increased summer precipitation benefits lichens growth (Johansen et al. 2019). The negative effects can be seen when the increased winter precipitation makes a thicker snow cover, which causes difficulties for reindeer to find food below the thick snow cover (Johansen et al. 2019). In particular, spring and autumn pastures may be exposed to new climatic conditions, and reindeer are going to face new challenges with increased snow cover and decreased lichen covers (Johansen et al. 2019). Rain-on-snow events are also becoming more

frequent, and which highly affects the food intake of reindeer, and can lead to mass starvations of whole herds (Forbes et al. 2016).

Research shows that climate change is already happening in the arctic areas, and that it most likely will lead to more drastic change in the future (AMAP 2017; Elmendorf et al. 2012). Reindeer herds are affected by the annual weather and snow conditions, and due to climate change, weather changes are going to be more unexpected and difficult to predict, causing problems for both reindeer and herders (Kumpula et al. 2015).

7 Conclusions

In this study I examined the effects that topography and grazing pressure differences have on the tundra vegetation patterns. The results indicate that there are significant vegetation differences between the Finnish and Norwegian sides of the fence. This means that summer and winter grazing affect the vegetation differently. Grazing history probably also has an impact on the vegetation differences. The size of impact that topography has also varies between the countries, the vegetation on the Norwegian side is more affected by topography than the vegetation on the Finnish side.

The vegetation differences are especially in the ground cover with more reindeer lichens on the Norwegian side and more bryophytes on the Finnish side. The ground layer is mostly affected by the grazing pressure, and after that the topography indices TPI50 and the elevation follows. Vascular plants are overall higher on the Norwegian side, and the height of vascular plants is first and foremost affected by the protection index for 50 m and elevation and the effect of grazing is lower. For evergreen dwarf shrubs BM and LAI is higher on the Finnish side, and so was the amount of litter and the Shannon's diversity index. My results are in line with the previous research found, and more research could potentially be done in more varying topography, in a bigger scale, and on a species level.

In this thesis, I did not examine the possible effects of climate change, and that could be included in further studies. My findings show that it is of great importance to protect lichens during snow-free periods from extensive reindeer grazing and trampling, to be able to maintain the arctic tundra ecosystems and protect the livelihood for the indigenous and local people.

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References

- Aalto, J., Pirinen, P., & Jylhä, K. (2016). New gridded daily climatology of Finland: permutation-based uncertainty estimates and temporal trends in climate. *Journal of Geophysical Research: Atmospheres*. 121(8). 3807-3823. DOI: 10.1002/2015JD024651
- Adler, P., Raff, D., Lauenroth, W. (2001). The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia*. 128. 465-479. DOI: 10.1007/s004420100737
- Alexander, C., Deák, B., Heilmeyer, H. (2016). Micro-topography driven vegetation patterns in open mosaic landscapes. *Ecological Indicators*. 60. 906-920. DOI: 10.1016/j.ecolind.2015.08.030
- AMAP. 2017. Snow, Water, Ice and Permafrost in the Arctic (SWIPA) 2017. Arctic Monitoring and Assessment Programme (AMAP). Oslo, Norway. Xvi + 269 pp.
- Bailey, D., Gross, J., Laca, E., Rittenhouse, L., Coughenour, M., Swift, D., Sims, P. (1996). Mechanisms That Result in Large Herbivore Grazing Distribution Patterns. *Journal of Range Management*. 49(5). 386-400. DOI: 10.2307/4002919.
- Berner, L.T., Massey, R., Jantz, P., Forbes, B.C., Macias-Fauria, M., Myers-Smith, I., Goetz, S. J. *et al.* (2020). Summer warming explains widespread but not uniform greening in the Arctic tundra biome. *Nature communications*. 11(1). 1-12. DOI: 10.1038/s41467-020-18479-5
- Bernes, C., Bråthen, K.A., Forbes, B.C. Speed, J.D.M., Moen, J. (2015). What are the impacts of reindeer/caribou (*Rangifer tarandus* L.) on arctic and alpine vegetation? A systematic review. *Environmental Evidence*. 4(4). DOI: 10.1186/s13750-014-0030-3
- Boehner, J. and Selige, T. (2006). Spatial prediction of soil attributes using terrain analysis and climate regionalisation. In: Boehner, J., McCloy, K.R., Strobl, J. [Ed.]: SAGA - Analysis and Modelling Applications, Goettinger Geographische Abhandlungen, Goettingen. 13-28.
- Boehner, J., Antonic, O. (2009). Land Surface Parameters Specific to Topo-Climatology. in Hengl, T. & Reuter, H.I. [Eds.]: Geomorphometry - Concepts, Software, Applications.
- Bråthen, K. Oksanen, J. (2001). Reindeer Reduce Biomass of Preferred Plant Species. *Journal of Vegetation Science*. 12 (4). 473-480. DOI: 10.2307/3236999.
- Breiman, L. (2001). Random forests. *Machine learning*. 45(1). 5-32.
- Bruun, H., Moen, J., Virtanen, R., Grytnes, J.A., Oksanen, L., Angerbjörn, A. (2006). Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. *Journal of Vegetation Science*. 17. 37 - 46. DOI: 10.1111/j.1654-1103.2006.tb02421.x.
- Chapin, F. S. III, M. S. Bret-Harte, S. E. Hobbie, and H. Zhong. 1996. Plant Functional Types as Predictors of Transient Responses of Arctic Vegetation to Global Change. *Journal of Vegetation Science*. 7(3). 347–358. doi:10.2307/3236278
- Chapin, F.S.III., Sturm, M., Serreze, M.C., McFadden, J.P., Key, J.R., Lloyd, A.H., McGuire, A.D., Rupp, T.S., Lynch, A.H., Schimel, J.P., Beringer, J., Chapman, W.L., Epstein, H.E., Euskirchen, E.S., Hinzman, L.D., Jia, G., Ping, C.-L., Tape, K.D., Thompson, C.D.C., Walker, D.A., Welker, J.M. (2005). Role of Land-Surface Changes in Arctic Summer Warming. *Science*. 310(5748), 657-660. DOI: 10.1126/science.1117368
- Cooper, E.J., Smith, F.M., Wookey, P.A. (2001). Increased Rainfall Ameliorates the Negative Effect of Trampling on the Growth of high Arctic Forage Lichens. *Symbiosis*. 31. 153-171.
- Cowles, J., Boldgiv, B., Liancourt, P., Petraitis, P., Casper, B. (2018). Effects of increased temperature on plant communities depend on landscape location and precipitation. *Ecology and Evolution*. 8(11). 5267-5278. DOI: 10.1002/ece3.3995

- Dearborn, K. D., Danby, R. K. (2020) Spatial Analysis of Forest–Tundra Ecotones Reveals the Influence of Topography and Vegetation on Alpine Treeline Patterns in the Subarctic. *Annals of the American Association of Geographers*. 110:1. 18-35. DOI:10.1080/24694452.2019.1616530
- Den Herder, M., Kytöviita, M.M. and Niemelä, P. 2003. Growth of reindeer lichens and effects of reindeer grazing on ground cover vegetation in a Scots pine forest and subarctic heathland in Finnish Lapland. *Ecography*. 26. 3-12. DOI: 10.1034/j.1600-0587.2003.03211.x
- Egelkraut, D., Barthelemy, H., Olofsson, J. (2020). Reindeer tramping promotes vegetation changes in tundra heathlands: Results from a simulation experiment. *Journal of Vegetation Science*. 31(3). 476–486. DOI: 10.1111/jvs.12871
- Eisenlohr, P.V., Alves, L.F., Bernacci, L.C. *et al.* (2013). Disturbances, elevation, topography and spatial proximity drive vegetation patterns along an altitudinal gradient of a top biodiversity hotspot. *Biodivers Conserv*. 22. 2767–2783. DOI: 10.1007/s10531-013-0553-x
- Elmendorf, S., Henry, G., Hollister, R., Björk, R., Boulanger-Lapointe, N., Cooper, E., Cornelissen, J., Day, T., Dorrepaal, E., Elumeeva, T., Gill, M., Gould, W., Harte, J., Hik, D., Hofgaard, A., Johnson, D., Johnstone, J., Jónsdóttir, I., Jorgenson, J., Wipf, S. *et al.* (2012). Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change*. 2(6). DOI: 10.1038/nclimate1465.
- Evans, R. (1996). Some Impacts of Overgrazing by Reindeer in Finnmark, Norway. *Rangifer*. 16(1). 3-19. DOI: 10.7557/2.16.1.1177.
- Forbes, B.C., Bølter, M., Müller-Wille, L., Hukkinen, J., Müller, F., Gunsley, N., Konstantinov, Y. (2006) Reindeer Management in Northernmost Europe: Linking Practical and Scientific Knowledge in Social-Ecological Systems. Springer, Berlin, Heidelberg. DOI: 10.1007/3-540-31392-3
- Forbes, B.C., Kumpula, T. (2009). The Ecological Role and Geography of Reindeer (*Rangifer tarandus*) in Northern Eurasia. *Geography Compass*. 3(4). 1356–1380. DOI: 10.1111/j.1749-8198.2009.00250.x
- Forbes, B.C., Kumpula, T., Meschytyb, N., Laptander, R., Macias-Fauria, M., Zetterberg, P., Verdonen, M., Skarin, A., Kim, K-Y., Boisvert, L. N., Stroeve, J.C., Bartsch A. (2016). Sea ice, rain-on-snow and tundra reindeer nomadism in Arctic Russia. *Biology Letters*. 12(11). DOI: 10.1098/rsbl.2016.0466
- Franklin, S.E. (2020). Interpretation and use of geomorphometry in remote sensing: a guide and review of integrated applications. *International Journal of Remote Sensing*. 41(19). 7700-7733. DOI: 10.1080/01431161.2020.1792577
- Guisan, A., Weiss, S.B., Weiss, A.D. (1999). GLM versus CCA spatial modeling of plant species distribution. *Plant Ecology*. 143: 107-122.
- Gurevitch, J., Scheiner, S., Fox, G. (2002). *The Ecology of Plants*. Sinauer Associates is an imprint of Oxford University Press; 3rd ed. Chapter 11.
- Helle, T., & Aspi, J. (1983). Effects of Winter Grazing by Reindeer on Vegetation. *Oikos*, 40(3), 337–343. DOI: 10.2307/3544306
- <https://opendata.luke.fi/fi/dataset/kosteusindeksi>; Murphy, P. N., Ogilvie, J., Connor, K., & Arp, P. A. (2007). Mapping wetlands: a comparison of two different approaches for New Brunswick, Canada. *Wetlands*. 27(4). 846-854. DOI: 10.1672/0277-5212(2007)27[846:MWACOT]2.0.CO;2
- Iversen M, Fauchald P, Langeland K, Ims RA, Yoccoz NG, Bråthen KA. (2014). Phenology and Cover of Plant Growth Forms Predict Herbivore Habitat Selection in a High Latitude Ecosystem. *PLoS ONE*. 9(6) e100780. DOI: 10.1371/journal.pone.0100780
- Järemo, J., Palmqvist, E. (2001). Plant compensatory growth: a conquering strategy in plant–herbivore interactions? *Evolutionary Ecology*. 15. 91-102. DOI: 10.1023/A:1013899006473
- Johansen, B., Tømmervik, H., Bjerkeog, J., Davids, C. (2019). Finnmarksvidda –kartlegging og overvåking av reinbeiter –STATUS 2018. Norut Northern Research Institute. Rapport 1/2019.

- Juutinen, S., Virtanen, T., Kondratyev, V., Laurila, T., Linkosalmi, M., Mikola, J., Nyman, J., Rasanen, A., Tuovinen, J.-P., & Aurela, M. (2017). Spatial variation and seasonal dynamics of leaf-area index in the arctic tundra-implications for linking ground observations and satellite images. *Environmental Research Letters*, 12(9), [095002]. DOI: 10.1088/1748-9326/aa7f85
- Kartverket. Available at: <https://www.kartverket.no/en/api-and-data/terrengdata> (Accessed 2020).
- Kitti, H., Forbes, B.C., Oksanen, J. (2008). Long- and short-term effects of reindeer grazing on tundra wetland vegetation. *Polar Biology*. 32(2). 253-261. DOI: 10.1007/s00300-008-0526-9.
- Kolari, T.H.M., Kumpula, T., Verdonen, M., Forbes, B.C., Tahvanainen T. (2019) Reindeer grazing controls willows but has only minor effects on plant communities in Fennoscandian oroarctic mires. *Arctic, Antarctic, and Alpine Research*. 51:1, 506-520, DOI: 10.1080/15230430.2019.1679940
- Kumpula, J., Kurkilahti, M., Helle, T., Colpaert, A. (2014). Both reindeer management and several other land use factors explain the reduction in ground lichens (*Cladonia* spp.) in pastures grazed by semi-domesticated reindeer in Finland. *Regional Environmental Change*. 14. 541–559. DOI: 10.1007/s10113-013-0508-5
- Kumpula, J., Siitari, J., Törmänen, H., Siitari, S. (2015). Porojen laitumet, ruokinta jatuottavuus poronhoitoalueen pohjoisosassa. Luonnonvarakeskus LUKE, Luonnonvara- ja biotalouden tutkimus 48/2015.
- Kumpula, T. (2006). Very High Resolution Remote Sensing Data in Reindeer Pasture Inventory in Northern Fennoscandia. *Reindeer management in Northernmost Europe*. 167-85. Berlin, Heidelberg: Springer. DOI: 10.1007/3-540-31392-3_9.
- Liaw, A., Wiener, M. (2002). Classification and regression by randomForest. *R news*, 2(3), 18-22.
- Löffler, J., Pape, R. (2008). Diversity Patterns in Relation to the Environment in Alpine Tundra Ecosystems of Northern Norway. *Arctic, Antarctic, and Alpine Research*. 40(2). 373-381. DOI: 10.1657/1523-0430(06-097)[LOEFFLER]2.0.CO;2
- Magurran, A. (2004). *Measuring Biological Diversity*. Blackwell Publishing, Oxford. Ch 4.
- Maliniemi, T., Kapfer, J., Saccone, P., Skog, A., Virtanen, R. (2018). Long-term vegetation changes of treeless health communities in northern Fennoscandia: Links to climate change trends and reindeer grazing. *Journal of Vegetation Science*. 29(3). 469-479. DOI: 10.1111/jvs.12630
- McMullin, R., Rapai, S. (2020). A review of reindeer lichen (*Cladonia* subgenus *Cladina*) linear growth rates. *Rangifer*. 40(1). 15-26. DOI: 10.7557/2.40.1.4636.
- Moen, J., Danell, Ö. (2003). Reindeer in the Swedish Mountains: An Assessment of Grazing Impacts. *AMBIO: A Journal of the Human Environment* 32(6), 397-402. DOI: 10.1579/0044-7447-32.6.397
- Nieminen, M., Heiskari, U. (1989). Diets of freely grazing and captive reindeer during summer and winter. *Rangifer*. 9(1). 17-34. DOI: 10.7557/2.9.1.771
- Niittynen, P., Heikkinen, R.K., Aalto, J., Guisan, A., Kemppinen, J., Luoto, M. (2020). Fine-scale tundra vegetation patterns are strongly related to winter thermal conditions. *Nature Climate Change*. 10. 1143-1148. DOI: 10.1038/s41558-020-00916-4
- Oksanen J., Blanchet F., Friendly M., Kindt R., Legendre P., McGlinn D., Minchin P., O'Hara R. B., Simpson G., Solymos P., Stevens M., Szoecs E. & Wagner H. (2019). Community Ecology Package: Ordination, Diversity and Dissimilarities. *Package 'vegan'*. Available at: <https://cran.r-project.org/web/packages/vegan/vegan.pdf> (Accessed Dec. 2020)
- Oksanen, L., Virtanen, R. (1995). Topographic, altitudinal and regional patterns in continental and suboceanic heath vegetation of northern Fennoscandia. *Acta Botanica Fennica*. 153. 1-80.
- Proulx, M., Mazumder, A. (1998). Reversal of Grazing Impact on Plant Species Richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecological Society of America*. 79(8). 2581-2592. DOI: 10.1890/0012-9658(1998)079[2581:ROGIOP]2.0.CO;2

- Räsänen, A., Juutinen, S., Aurela, M., Virtanen, T. (2019) Predicting aboveground biomass in Arctic landscapes using very high spatial resolution satellite imagery and field sampling. *International Journal of Remote Sensing*. 40(3). 1175-1199. DOI: 10.1080/01431161.2018.1524176
- Räsänen, A., Wagner, J., Hugelius, G., Virtanen, T. (2021). Aboveground biomass patterns across treeless northern landscapes. *International Journal of Remote Sensing*. 42(12). 4536-4561, DOI: 10.1080/01431161.2021.1897187
- Ravolainen, V. T., Bråthen, K. A., Yoccoz, N. G., Nguyen, J. K., & Ims, R. A. (2014). Complementary impacts of small rodents and semi-domesticated ungulates limit tall shrub expansion in the tundra. *Journal of Applied Ecology*, 51(1), 234-241. DOI: 10.1111/1365-2664.12180
- Sappington, J. M., Longshore, K. M., Thompson, D. B. (2007). Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. *The Journal of wildlife management*. 71(5). 1419-1426.
- Sundqvist, M. K., Moen, J., Björk, R. G., Vowles, T., Kytöviita, M. M., Parsons, M. A., & Olofsson, J. (2019). Experimental evidence of the long-term effects of reindeer on Arctic vegetation greenness and species richness at a larger landscape scale. *Journal of Ecology*, 107(6), 2724-2736. DOI: 10.1111/1365-2745.13201
- Suominen, O., Olofsson, J. (2000). Impacts of semi-domesticated reindeer on structure of tundra and forest communities in Fennoscandia: a review. *Annales Zoologici Fennici*. 37(4). 233-249.
- Van der Wal, R. (2006). Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. *Oikos*. 114(1). 177-186. DOI: 10.1111/j.2006.0030-1299.14264.x
- Virtanen, R., Oksanen, L., Oksanen, T., Cohen, J., Forbes, B.C., Johansen, B., Käyhkö, J., Olofsson, J., Pulliainen, J., Tømmervik, H. (2016). Where do the treeless tundra areas of northern highlands fit in the global biome systems: toward an ecologically natural subdivision of the tundra biome. *Ecology and Evolution*. 6(1). 143-158. DOI: 10.1002/ece3.1837
- Virtanen, R., Oksanen, L., Razzhivin, V. (1999). Topographic and regional patterns of tundra heath vegetation from northern Fennoscandia to the Taimyr Peninsula. *Acta Botanica Fennica*. 167. 29-83.
- Vowles, T., Lovehø, C., Molau, U., Björk, R.G. (2017). Contrasting impacts of reindeer grazing in two tundra grasslands. *Environmental Research Letters*. 12(3). DOI: 10.1088/1748-9326/aa62af/
- Walker, D.A. (2002). Hierarchical subdivision of Arctic tundra based on vegetation response to climate, parent material and topography. *Global Change Biology*. 6(S1). 19-34. DOI: 10.1046/j.1365-2486.2000.06010.x
- Wang, P., de Jager, J., Nauta, A. et al. (2019). Exploring near-surface ground ice distribution in patterned-ground tundra: correlations with topography, soil and vegetation. *Plant Soil*. 444. 251–265. DOI: 10.1007/s11104-019-04276-7
- Wei, T., Simko, V., Levy, M., Xie, Y., Jin, Y., Zemla, J. (2017). Corrplot: Visualization of a Correlation Matrix. Available at: <https://CRAN.R-project.org/package=corrplot> (Accessed Dec.2020)
- Yokoyama, R., Shirasawa, M., Pike, R. J. (2002). Visualizing topography by openness: a new application of image processing to digital elevation models. *Photogrammetric engineering and remote sensing*. 68(3). 257-266.
- Zedda L., Rambold G. (2015) The Diversity of Lichenised Fungi: Ecosystem Functions and Ecosystem Services. In: Upreti D., Divakar P., Shukla V., Bajpai R. (eds) Recent Advances in Lichenology. Springer, New Delhi. DOI: 10.1007/978-81-322-2235-4_7

Appendices

Appendix 1: Plants species by functional group

Evergreen dwarf shrubs

- *Empetrum nigrum*, (ssp. *hermaphroditum*)
- *Phyllodoce caerulea*
- *Linnaea borealis*
- *Vaccinium vitis-idaea*
- *Loiseleuria procumbens*

Deciduous dwarf shrubs

- *Arctostaphylos alpina*
- *Vaccinium myrtillus*
- *Vaccinium uliginosum*
- *Salix polaris*
- *Salix herbacea*
- *Salix glauca*

Dwarf birch

- *Betula Nana*

Forbs

- *Lysimachia europaea*
- *Lycopodium clavatum*, (ssp. *monostachyon*)
- *Diphysastrum alpinum*
- *Pedicularis lapponica*
- *Erigeron uniflorus*
- *Solidago virgaurea*

Graminoids

- *Carex bigelowii*
- *Carex aquatilis*
- *Carex lapponica* (cf. *canescens*)
- *Calamagrostis neglecta*
- *Nardus stricta*
- *Festuca ovina*
- *Juncus trifidus*
- *Juncus filiformis*
- *Deschampsia flexuosa*

Reindeer lichens

- *Cladonia arbuscula*
- *Cladonia rangiferina*
- *Cladonia stellaris*

Lichens

- *Alectoria* sp.
- *Cetraria ericetorum*
- *Cetraria islandica*
- *Cetraria muricata*
- *Cetraria nigricans*
- *Cetraria* sp.
- *Cladonia borealis*
- *Cladonia* cf. *bellidiflora*
- *Cladonia coccifera*
- *Cladonia cornuta*
- *Cladonia crispata*
- *Cladonia deformis*
- *Cladonia fimbriata*
- *Cladonia gracilis*
- *Cladonia gracilis* ssp. *elongata*
- *Cladonia maxima*

- *Cladonia pleurota*
- *Cladonia sp.*
- *Cladonia subfurcata*
- *Cladonia sulphuriana*
- *Cladonia uncialis*
- *Flavocetraria cuccullata*
- *Flavocetraria nivalis*
- *Imadophila sp.*
- *Lichen crust*
- *Nephroma arcticum*
- *Nephroma sp.*
- *Ochrolechia frigida*
- *Peltigera sp.*
- *Solorina crocea*
- *Sphaerophorus globosus*
- *Stereocaulon alpinum*

Bryophytes

- *Dicranum elongatum*
- *Dicranum scoparium*
- *Hepaticae sp.*
- *Pleurozium schreberi*
- *Pohlia nutans*
- *Pohlia sp.*
- *Polytrichum commune*
- *Polytrichum juniperinum*
- *Polytrichum strictum*
- *Ptilidium ciliare*

Appendix 2: Scatter plots of vegetation groups and topography indices

